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ORIGINAL PAPER

Quantity discrimination in angelfish (*Pterophyllum scalare*) is maintained after a 30-s retention interval in the large but not in the small number range

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Abstract The ability to discriminate between sets that differ in the number of elements can be useful in different contexts and may have survival and fitness consequences. As such, numerical/quantity discrimination has been demonstrated in a diversity of animal species. In the laboratory, this ability has been analyzed, for example, using binary choice tests. Furthermore, when the different number of items first presented to the subjects are subsequently obscured, i.e., are not visible at the moment of making a choice, the task requires memory for the size of the sets. In previous work, angelfish (*Pterophyllum scalare*) have been found to be able to discriminate shoals differing in the number of shoal members both in the small (less than 4) and the large (4 or more) number range, and they were able to perform well even when a short memory retention interval (2–15 s) was imposed. In the current study, we increased the retention interval to 30 s during which the shoals to choose between were obscured, and investigated whether angelfish could show preference for the larger shoal they saw before this interval. Subjects were faced with a discrimination between numerically small shoals (≤4 fish) and also between numerically large (≥4 fish) shoals of conspecifics. We found angelfish not to be able to remember the location of larger versus smaller shoals in the small number range, but to exhibit significant memory for the larger shoal in the large number range as long as the ratio between these shoals was at least 2:1. These results, together with prior findings, suggest the existence of two separate quantity estimation systems, the object file system for small number of items that does not work with the longer retention interval and the analogue magnitude system for larger number of items that does.

Keywords Quantity discrimination · Social preference · Angelfish · Working memory · Numerical cognition · Continuous variables

Introduction

A diversity of nonhuman animals, as well as humans, possess nonverbal ability to discriminate between different quantities of items (reviewed in Feigenson et al. 2004). This ability has evolutionary advantages since it allows individuals to distinguish places with more food (Lucon-Xiccato et al. 2015), the size of the rival groups (Benson-Amram et al. 2011), the number of mates (Lemaître et al. 2011), the number of shoaling members for protection (Agrillo et al. 2007), the brood size for parental investment (Forsaktar et al. 2016), the more vulnerable group of prey for hunting (Panteleeva et al. 2013) or the larger social group more ideal for protection in potentially dangerous environments (Hager and Helfman 1991). Given such advantages, it is not surprising that the ability to discriminate between sets of items differing in number has been found in a wide range of animal species (reviewed in Reznikova and Ryabko 2011). According to some authors, there are two distinct representational systems to account for the discrimination of number/quantity: one system for sets composed of small number of items (up to 3 or 4); and another for large number of items (at least 4) (see

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Feigenson et al. 2004). For small number discrimination, a system called the object file system (OFS) is believed to act. This system appears to rely upon representation of each item of the sets of items compared and allows the discrimination of the sets based upon absolute numerical difference (Feigenson et al. 2002a). When the two sets to be compared have a larger number of items, the analogue magnitude system (AMS) is thought to be used. This system relies on ratio and not absolute numerical difference between the compared sets. Thus, the AMS follows Weber's law: the larger the ratio of the larger set to the smaller set (the larger the relative difference between the compared sets), the more accurate and reliable discrimination becomes.

Most studies examining numerical abilities in nonhuman animals have been carried out in the laboratory. Many studies on nonhuman species exploit spontaneous choice tasks, in which subjects freely choose between alternatives. Often, the contrasted items are presented simultaneously and are actually present, visible or detectable, at the moment of choice, a method that has been successfully employed with a large number of species including mammals, birds and even amphibians (Hanus and Call 2007; Krusche et al. 2010; Abramson et al. 2011; Baker et al. 2012; Garland et al. 2012; Bogale et al. 2014; Stancher et al. 2015; Tornick et al. 2015; Bánszegi et al. 2016; Cox and Montrose 2016; Kelly 2016).

However, recently, the question of storing and comparing the quantities mentally, i.e., the mental representation of quantities (memory), has also started to be examined. In spontaneous choice tests, the items in the sets may be hidden from view of the subjects after having being presented in full view or after having being displayed one by one sequentially. In these tasks, choice is tested while the previously presented numerically different items are not observable, i.e., numerical or quantity-related information on the items is not available at the time of choice. Therefore, appropriate response requires mental representation of the item sets discriminated (Hauser et al. 2000; Feigenson et al. 2002a; Hanus and Call 2007; Hunt et al. 2008; Evans et al. 2009; Rugani et al. 2009; Uller and Lewis 2009; Utrata et al. 2012; Barnard et al. 2013; Mahamane et al. 2014; Ujfalussy et al. 2014). Tests in which full presentation of the contrasted item sets is followed by lack of visual access to these sets during the moment of choice, have been successfully employed with only a few fish species, namely redtail splitfin *Xenotoca eiseni* (Stancher et al. 2013) and zebrafish *Danio rerio* (Potrich et al. 2015), indicating that individuals of at least these fish species were able to maintain representation of the contrasted quantities in their working memory. In these studies, two numerically different shoals of conspecifics were presented at each end of an experimental tank.

Thereafter, shoals were occluded leaving visible an equal number of conspecifics. After a delay of 5 or 30 s, experimental fish were able to approach the location where the larger shoal was previously seen, thus making their choice on the basis of short-term memory.

We have been studying quantity estimation abilities of angelfish (*Pterophyllum scalare)* and have utilized both the direct spontaneous choice task and, more recently, the task involving no visual access to the full shoals at the time of choice. We have found juvenile angelfish to be able to discriminate shoals comprising different numbers of conspecifics both in the small and in the large number range in a comparable manner when the stimulus shoals were in full view during the choice (Gómez-Laplaza and Gerlai 2011a, b) or when presentation of the stimulus shoals was followed by obstructing the view of these shoals (Gómez-Laplaza and Gerlai 2015, 2016a, b). The latter consisted of a modification from the method developed by Stancher et al. (2013) and included presentation of a single stimulus fish on each lateral side of the experimental aquarium at the moment of choice (after an interval of stimulus occlusion following full view of the shoals). Thus, test fish had to choose while viewing only one individual of each stimulus shoal. In our previous studies, we allowed a period of stimulus occlusion (retention interval) to range from 2 to 15 s (Gómez-Laplaza and Gerlai 2015, 2016a, b). We found angelfish to be able to discriminate numerically different shoals when the shoals were of small size (4 vs. 1, 3 vs. 1, 2 vs. 1, 3 vs. 2 and 4 vs. 2), but they failed in the comparisons 4 versus 3, 5 versus 4 and 6 versus 4. Also, angelfish when presented with numerically large shoals of conspecifics preferred the larger of two shoals when the shoals differed by a 2:1 or higher ratio, but not when the shoals differed by a 3:2 or 4:3 ratio. Thus, according to Weber's law, as the ratio between the larger and the smaller shoal approached one, the performance became poorer. These results were comparable with those found in angelfish when the contrasted shoals were in full view at the time of choice. We concluded that angelfish were able to use short-term memory in the discrimination, i.e., they had mental representation of some features of the shoals, including information on the size and location of the contrasted shoals.

Angelfish in the wild forms shoal of 15–20 individuals outside of the breeding season, mainly as defense against predators (Praetorius 1932). This freshwater, sexually monomorphic, cichlid species lives in shallow, turbid waters with dense vegetation, in areas subjected to flooding. The complex nature of its environment may lead angelfish to occasionally get separated from shoals, which may result in increased vulnerability to predators (Praetorius 1932). Thus, remembering the location and size of shoals may have adaptive significance for angelfish (Ioannou et al. 2008). Our

previous results, showing preference for larger shoals in angelfish, also support this notion.

In a previous study, we also found that the precision of discrimination slightly decreased as the retention interval increased (Gómez-Laplaza and Gerlai 2016b). However, we do not yet know whether angelfish are capable of maintaining information in their memory on shoal size and location longer than 15 s. In the present study, we increased the memory demand by doubling the required retention interval during which angelfish had no visual access to the contrasted shoals. That is, the test subjects had to remember the size and location of previously shown shoals for 30 s. We note that such a long retention interval has not been previously imposed in angelfish and rarely in any study dealing with numerical abilities in fish species. The two exceptions are studies by Stancher et al. (2013) conducted with redtail splitfin and by Potrich et al. (2015) conducted with zebrafish. However, in these studies, unlike in our current one, fish could see not one but an equal number of multiple conspecifics during testing. Furthermore, in these prior studies, performance in the large number range was not tested (Stancher et al. 2013) or only a few contrasts were presented (Potrich et al. 2015). Using this longer retention interval, we intend to examine the potential memory limits of numerical representation and quantity discrimination abilities of angelfish both when small and large numbers of items (members in stimulus shoals) are contrasted. Thus, our study may be able to distinguish the use of object file or analogue magnitude systems in angelfish. In Experiment 1, we explored whether angelfish were able to distinguish between the location of a previously presented shoal of conspecifics and an empty tank. A positive result would indicate that the procedure is appropriate for the analysis of working memory of location of a shoal in angelfish, a minimum requirement for our study. In Experiment 2, we explored whether angelfish could remember where the numerically larger of the two previously seen shoals was when the number of members of each of these shoals was within the small number range. Finally, in Experiment 3 we investigated whether angelfish could discriminate the locations of previously seen shoals when the number of the members of these shoals was in the larger number range and explored whether the ability to discriminate followed Weber's law.

Materials and methods

Subjects

Angelfish used in the experiments were juveniles (3.0–3.3 cm standard length) to avoid possible con-founding effects arising from territoriality, courtship or other forms of reproduction-related behaviors. Fish were obtained from local commercial suppliers and housed in the laboratory in glass-holding aquaria (60 × 30 × 40 cm deep) in groups of 20–25 individuals. The aquaria were filled with dechlorinated tap water, kept at 26 ± 1 °C using thermostat-controlled heaters. Each aquarium was illuminated by a 15-W white fluorescent light tube placed above the tank, and a 12:12 h light/dark cycle was maintained with lights on at 08.30 h. External filters continuously cleaned the aquaria, which had a 2-cm-deep gravel substratum. The fish were fed twice daily (at 10.00 and at 18.00 h) on commercial fish food (JBL GALA, JBL GmbH & Co. KG, Neuhofen, Germany). Test fish and stimulus fish were randomly distributed between the aquaria and housed separately with no visual communi-cation being possible between fish across the separate aquaria. A minimum of a 2-week acclimation period under the above conditions was allowed prior to testing. All fish were returned to the supplier at the end of the study.

Apparatus

The experimental apparatus was identical to the one we used in previous dichotomous shoal-choice studies with angelfish (Gómez-Laplaza and Gerlai 2016a, b). It con-sisted of a test aquarium, with one stimulus aquarium (30 × 30 × 40 cm deep) positioned at each end. The test aquarium was identical in all respects to the holding aquaria, and test, stimulus and holding aquaria were all maintained under the same conditions. In the stimulus aquaria, an opaque divider isolated a 10-cm compartment where the stimulus shoals were placed. An additional opaque divider separated the stimulus compartment into two equal independent halves facing the test aquarium. In one half, a stimulus angelfish was placed, and in the other the rest of the members of the stimulus shoals (Fig. 1). To prevent the fish from being disturbed by external visual stimuli, all exterior walls of the aquaria that were not adjacent to other aquaria were lined with white cardboard, except for the front.

Five vertical lines drawn on the front and back walls of the test aquarium, 10 cm from each other, delimited six equal zones. They allowed measurements of the test fish's movements and position. The two 10-cm zones closest to the stimulus aquaria were considered to be the preference zones. At least three-quarters of the body length of the fish had to be within the boundary for the fish to be considered being inside such zones. Swimming activity of test fish was measured as the frequency (number of times) the fish crossed the lines.
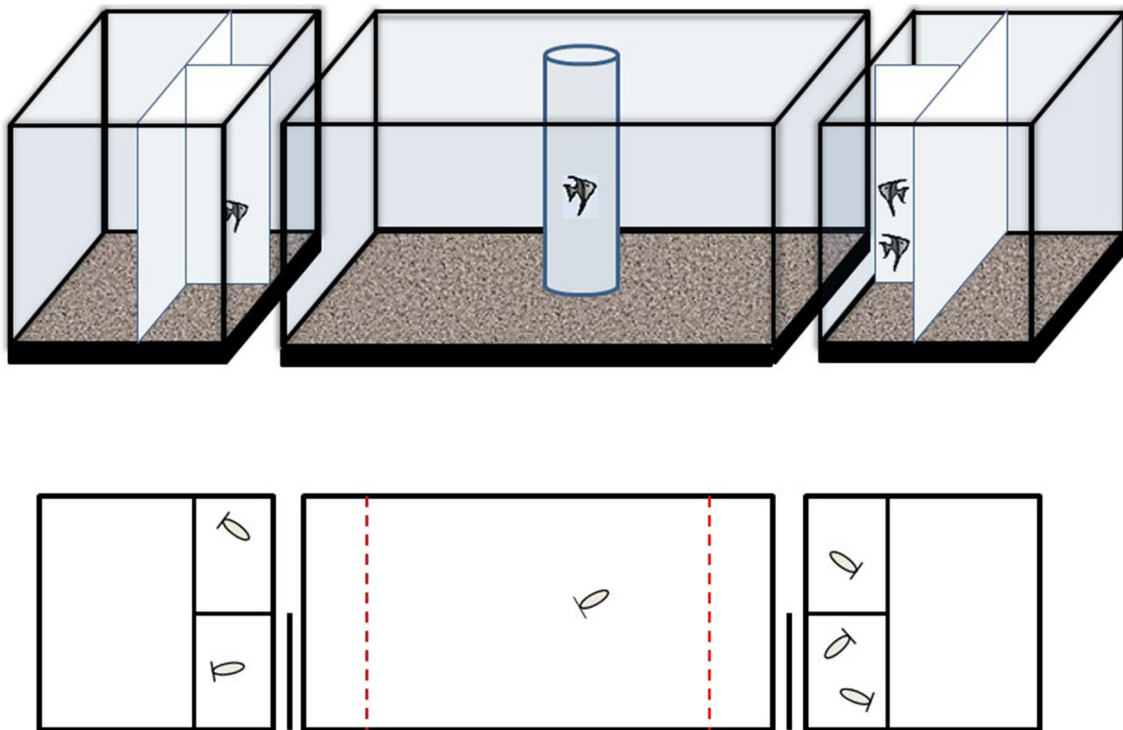
Fig. 1 Front (*upper*) and top (*lower*) views of the experimental apparatus showing the central test tank and the two stimulus tanks at each end of the test tank. In the stimulus tanks, opaque white dividers were used to delimit a 10-cm compartment close to the test tank, where the stimulus shoals were presented to the test fish. An additional opaque white panel divided this compartment in half: in one half, a single stimulus angelfish was placed, and in the other half the rest of the members of the stimulus shoals. Opaque white barriers were used to visually isolate the two stimulus tanks (with the stimulus shoals) from the test tank during the retention interval (30 s). These barriers were moved backward so as to present a single stimulus fish on both sides when preference tests commenced, while the rest of the members of the shoal were kept hidden. The time the test fish spent within 10 cm of the stimulus shoals (*dashed lines*: preference zones) was recorded

Procedure

The procedure employed was similar to the one already utilized and described in detail elsewhere (Gómez-Laplaza and Gerlai 2016a, b). Briefly, juvenile angelfish were individually tested in a choice between two numerically different shoals of conspecifics presented simultaneously and positioned in the stimulus aquaria on opposite sides of the test aquarium. One fish of each of the stimulus shoals was individually placed into the rear part of each of the corresponding stimulus compartments, whereas the rest of the members of each of the stimulus shoals were placed into the front part of the stimulus compartments from the observer's point of view (Fig. 1). Fish in the stimulus shoals were allowed a 10-min period to habituate to the stimulus aquaria. The positioning of the larger versus smaller shoal was initially randomized for each test fish and subsequently counterbalanced across trials. Trials took place 15–30 min after feeding in the morning.

Test fish, randomly chosen, were introduced singly to the center of the test aquarium via a transparent, open-ended, plastic cylinder (7 cm diameter), in which they were kept for 3 min. During this acclimation period of time, test fish could see the full stimulus shoals presented in the stimulus compartments at both sides of the experimental aquarium from an equal distance. When in the cylinder, all test fish oriented toward both shoals. At the end of this period, opaque white barriers were placed outside the two end sides of the test aquarium to visually isolate test fish from all stimulus fish. After a 30-s period of time with no stimulus fish in view (retention interval), the opaque barriers were moved backward leaving just one stimulus fish of each shoal (the one placed in the rear compartment from the observer's point of view) visible for the test fish, to trigger shoaling response (and, thus, a choice) from the experimental angelfish. The transparent cylinder was gently removed, and the test fish thus released and allowed to swim freely. Shoaling preference was recorded over a 15-min period and was defined as the time spent by the test fish in the 10-cm preference zones, that is, within 10 cm from the wall adjacent to the stimulus shoal aquaria on either side. Behavioral responses of the test fish were recorded with a video camera (Sony video Hi8, model CCD-TR750E) positioned 180 cm away in front of the tank concealed behind a blind. The recordings were later replayed for analysis.

Approaching and staying in the zone close to the previously visible larger shoal would be expected if test fish remembered the location of the larger versus smaller shoal.

Experiment 1 was conducted similarly, but here the choice offered was between four similarly sized conspecifics on one side versus no fish on the other side. Accordingly, in Experiment 1, after the 30-s retention interval with no fish in view, the opaque barriers were not moved, and no stimulus fish was presented at either side of the tank during behavioral recording session.

After each trial, the experimental aquaria were cleaned to eliminate potential odor cues before being replenished with dechlorinated tap water for the next behavioral recording session. Individual fish were tested only once, and none of the fish in the stimulus shoals were used as test fish and vice versa. Within each experiment, the order of testing was randomized according to different treatment (numerical ratio) conditions. Stimulus shoals were rearranged after each trial, so that each test fish was exposed to stimulus shoals with different individual members in them.

Statistical analysis

We recorded the time spent in each preference zone, the first preference zone selected (first choice), the frequency of entries to the preference zones, the latency to enter the preference zones and swimming activity.

In each experiment, the data were tested for normality (using the Kolmogorov–Smirnov one-sample test) and equality of variance (using Levene's test) before analysis. Most data conformed to assumptions, and those that did not (e.g., latency data) were log-transformed to meet assumptions of normality and homogeneity of variance. The time spent in the preference zones (sec) was considered as a measure of each test fish's preference for a particular stimulus shoal. A preference index was calculated for each test fish as the proportion of time test fish spent close to the larger stimulus shoal relative to the total time spent in both preference zones. Before statistical analysis, a criterion of exclusion was applied as follows: During the binary choice, test subjects had to enter both preference zones at least once; otherwise, they were excluded from the experiments and replaced by another fish. In Experiment 2, five subjects ($\sim$7%) were excluded and replaced, whereas in Experiment 3, two subjects ($\sim$2%) did not meet the criterion.

A one-sample one-tailed t test was employed to investigate whether the observed preference index was significantly ($p \leq 0.05$) higher than chance (50%). The Holm–Bonferroni sequential correction method was employed to minimize type I error (Holm 1979). A one-way ANOVA for independent samples was used to analyze the effect of the treatments on preference, and in case of a significant effect, Tukey's honestly significant difference (HSD) post hoc multiple comparison tests were performed to determine significant differences among treatment groups. A binomial test was performed to determine whether the first choice made by test fish was above-chance level, and latency data were analyzed using a paired t test. In Experiment 2, the criterion of variance homogeneity was not met for swimming activity (Levene's test: $p = 0.004$), and data were log-transformed before performing ANOVA and Tukey's HSD post hoc tests.

Experiment 1

Shoal discrimination after 30-s retention interval (control: 4 vs. 0 fish)

The aim of this experiment was to determine whether angelfish, under the present conditions of memory load, were able to remember the location of the group of four fish without seeing any stimulus fish to trigger the response. The side of the stimulus shoal was chosen randomly for the first experimental subject, after which the location of the stimulus shoal versus the empty stimulus tank was systematically alternated across the test fish to avoid potential side preferences. A total 12 experimental fish were tested.

Results

In this control treatment, test fish spent significantly more time in the preference zone near the compartment previously containing a shoal of four conspecifics than near the compartment previously containing no fish (mean proportion of time (preference index) $\pm$ SEM: 0.8109 $\pm$ 0.0622; $t_{11} = 5.00$, $p < 0.001$). This result indicated that the task was appropriate for angelfish. The results for the other behavioral parameters measured are shown in Table 1.

Experiment 2

Discrimination of small quantities (≤4) after a 30-s retention interval

In this experiment, we investigated whether angelfish could exhibit a preference toward the location at which they previously saw the larger of two small shoals. The two stimulus shoals had a number of members within the small number range (≤4 fish). The involvement of memory was necessary for a successful discrimination of the spatial location of the numerically larger shoal, because at the time of choice, only one fish of each of the contrasted shoals was visible to the subjects and the two shoals had been hidden from view for 30 s.

Table 1 Performance of angelfish ($N = 12$) when faced with the different contrasts

Contrasts	Initial choice (out of 12 test fish)[a]			Latency[b]				Swimming activity Mean ± SEM
	Smaller shoal	Larger shoal	Binomial test (p)	Smaller shoal	Larger shoal	t test		
						t_{11} value	probability (p)	
Experiment 1								
4 versus 0	4	8	>0.05	455.92 ± 129.39	94.83 ± 49.72	2.404	0.035	58.50 ± 28.32
Experiment 2								
4 versus 1	4	8	>0.05	204.33 ± 68.61	122.75 ± 43.23	0.953	>0.05	25.33 ± 4.17
3 versus 1	4	8	>0.05	190.25 ± 54.99	111.33 ± 51.08	0.974	>0.05	53.42 ± 6.92
2 versus 1	8	4	>0.05	132.25 ± 56.49	276.50 ± 77.02	1.277	>0.05	54.33 ± 10.06
4 versus 2	5	7	>0.05	143.67 ± 53.20	54.58 ± 20.26	1.342	>0.05	86.25 ± 9.97
3 versus 2	4	8	>0.05	160.42 ± 50.73	166.75 ± 63.22	0.062	>0.05	91.67 ± 19.65
4 versus 3	8	4	>0.05	38.00 ± 17.53	113.75 ± 42.87	1.474	>0.05	63.00 ± 8.92
Experiment 3								
12 versus 4	2	10	0.039	140.17 ± 37.54	30.08 ± 13.77	2.440	0.033	51.00 ± 6.27
10 versus 4	2	10	0.039	196.50 ± 47.19	27.17 ± 18.57	2.985	0.012	68.92 ± 8.94
10 versus 5	3	9	>0.05	159.17 ± 42.69	111.17 ± 56.45	0.542	>0.05	55.58 ± 9.86
8 versus 4	3	9	>0.05	328.08 ± 71.62	72.67 ± 27.42	2.818	0.017	40.17 ± 7.97
9 versus 5	2	10	0.039	135.25 ± 33.88	46.08 ± 30.56	1.645	>0.05	62.17 ± 9.40
8 versus 5	3	9	>0.05	226.08 ± 62.53	85.75 ± 42.26	1.524	>0.05	73.83 ± 10.18
6 versus 4	5	7	>0.05	85.67 ± 24.18	121.83 ± 46.91	0.571	>0.05	61.75 ± 9.12

In each contrast, only one stimulus fish of each shoal was visible for the experimental fish during the test

[a] Number of experimental fish whose first choice was one or the other stimulus shoal

[b] Latency to enter the preference zone near one or the other stimulus shoal. The results for frequency of entries to the preference zones are not presented since differences were not significant in any contrasts (but see results section for Experiment 2). Descriptive statistics include mean ± SEM. The tests used to compare the scores are also included

Methods

Test fish matched for standard length (± 0.20 cm) with the stimulus fish were presented with six different binary choices. The stimuli presented consisted of the following numerical comparisons: 4 fish versus 1 fish, 4 fish versus 2 fish, 4 fish versus 3 fish, 3 fish versus 1 fish, 3 fish versus 2 fish and 2 fish versus 1 fish. Thus, the range of the numerical ratios (large shoal/small shoal) varied from 4:1 to 1.33:1, whereas the absolute numerical difference between the stimulus shoals size varied between 1 and 3 fish. Sample sizes were 12 experimental fish for each of the six sets of choices (i.e., a total of 72 experimental fish were tested).
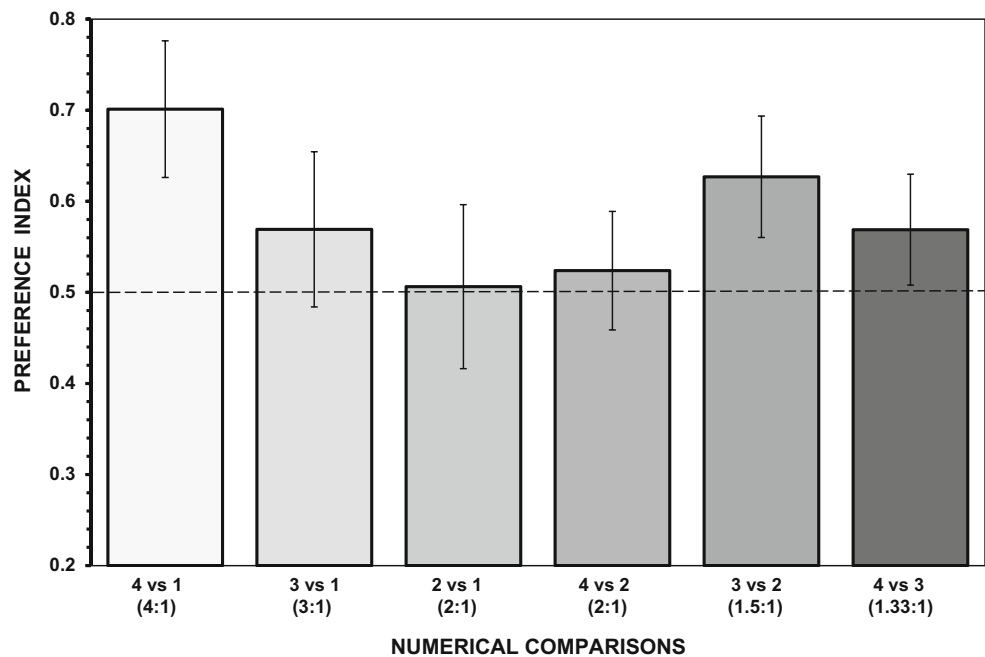
Results

After a 30-s retention interval, angelfish fish failed to distinguish between small shoals of conspecifics whose numerical size was in the small number range. No significant preference could be detected for the larger of the two

shoals in any of the six contrasts tested (t tests with Holm–Bonferroni correction: 4 vs. 1, $t_{11} = 2.682$, $p = 0.064$; 3 vs. 1, $t_{11} = 0.811$, $p = 0.652$; 2 vs. 1, $t_{11} = 0.069$, $p = 0.473$; 4 vs. 2, $t_{11} = 0.365$, $p = 0.722$; 3 vs. 2, $t_{11} = 1.902$, $p = 0.209$ and 4 vs. 3, $t_{11} = 1.132$, $p = 0.564$; Fig. 2). Likewise, fish did not show a significant preference for first entering the preference zone close to the larger stimulus shoal in any of the contrasts (binomial test $p_s > 0.05$) (see also Table 1).

One-way ANOVA confirmed the above findings and showed no significant difference among the performance of experimental fish obtained for the six different contrasts ($F_{5,66} = 0.925$, $p = 0.471$). However, significant differences in locomotor activity were detected among fish exposed to the six different contrasts ($F_{5,66} = 6.082$, $p < 0.001$). Fish in contrast 4 versus 1 swam significantly less compared to fish exposed to all other contrasts (Tukey's HSD test: $p_s \leq 0.023$), with the exception of the contrasts 2 versus 1, where only a marginal nonsignificant difference was found ($p = 0.058$). Furthermore, and sup-

Fig. 2 Mean ± SEM proportion of time (preference index) spent by test fish in the 10-cm preference zone near the larger stimulus shoal after a retention interval of 30 s when shoals with a small number of members were presented in dichotomous choice test. Values above 0.5 indicate a preference for the numerically larger shoal. No significant departure from the null hypothesis of no preference was found in any of the comparisons

porting these results, the frequency of entries to the preference zone close to the larger shoal was also found to be significantly different among fish exposed to the different contrasts ($F_{5,66} = 6.696$, $p < 0.001$). The frequency was significantly lower in experimental angelfish exposed to contrast 4 versus 1 relative to angelfish exposed to all other contrasts ($p_s \leq 0.042$), except the 2 versus 1 ($p = 0.831$). These results reflect the greater tendency of experimental angelfish in the contrast 4 versus 1 to stay close to the larger shoal for longer time, instead of moving from one stimulus shoal to the other, a conclusion also supported by the apparent trend seen in Fig. 2.

Experiment 3

Discrimination of large quantities (≥4) after a 30-s retention interval

The results of Experiment 2 showed that angelfish, with a 30-s retention interval imposed, were not able to reliably discriminate between numerically small shoals. In Experiment 3, we investigated whether angelfish could discriminate shoals in the large number range expected to engage the analogue magnitude system, also employing the 30-s-long retention interval. The binary shoal-choice test consisted of the following contrasts: 6 fish versus 4 fish, 8 fish versus 5 fish, 8 fish versus 4 fish, 9 fish versus 5 fish, 10 fish versus 5 fish, 10 fish versus 4 fish and 12 fish versus 4 fish. These contrasts correspond to ratios ranging from 1.5:1 to 3:1, while the numerical differences between stimulus shoals

ranged from 2 to 8 fish. Twelve experimental fish were tested in each of these seven contrast conditions, a total of 84 experimental fish. The experimental protocol and dependent variables were as described in Experiment 2.

Results

When the ratio between the contrasted shoals (larger shoal/ smaller shoal) was 2:1, we found angelfish to significantly prefer the larger shoal. When the ratio was lower, however, the preference index was found indistinguishable from chance (Fig. 3). Thus, in the contrasts 6 versus 4 ($t_{11} = 0.735$, $p = 0.239$), 8 versus 5 ($t_{11} = 2.173$, $p = 0.079$) and 9 versus 5 ($t_{11} = 1.336$, $p = 0.209$), no significant preference was detected (Holm–Bonferroni corrected t tests). Whereas for contrasts whose ratios were between 2:1 and 3:1; i.e., from 8 versus 4 to 12 versus 4, the preference index was found to be significantly above chance (t tests with Holm–Bonferroni correction: $t_{11} = 4.193$–3.239, $p_s = 0.005$–0.019; Fig. 3), demonstrating that experimental fish spent significantly more time in the preference zone close to the larger shoal.

Using the binomial test, we also analyzed the first choice made by the experimental fish after having been released from the transparent cylinder (Table 1). A preference for the larger shoal was shown by 10 out of the 12 fish in the contrasts 12 versus 4, 10 versus 4 and 9 versus 5 (a significant preference, $p = 0.039$), whereas 9 out of 12 fish initially chose the larger shoal in the rest of the contrasts ($p_s > 0.05$), and in 6 versus 4, only 7 out of 12 fish first chose the larger shoal. No significant difference among

Fig. 3 Mean ± SEM proportion of time (preference index) spent by test fish in the 10-cm preference zone near the larger stimulus shoal after a retention interval of 30 s when shoals with a large number of members were presented in dichotomous choice test. Values above 0.5 indicate a preference for the numerically larger shoal. Significant departure from the null hypothesis of no preference is indicated by asterisks: ***$P = 0.005$, **$P < 0.01$, *$P < 0.05$
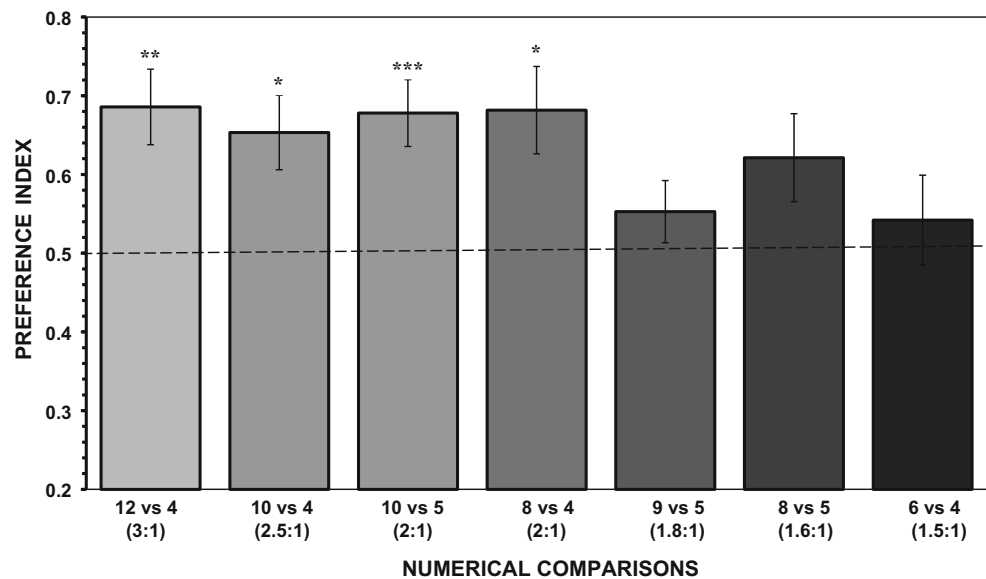
groups of fish exposed to the different contrasts was revealed in the magnitude of the preferences (one-way ANOVA: $F_{6,77} = 1.504$, $p = 0.188$). But groups of fish (pooled) exposed to contrasts with a ratio lower than 2:1 versus those equaling or exceeding this ratio did differ from each other significantly ($F_{1,82} = 7.576$, $p = 0.007$). Results also indicated that fish exhibited a significantly shorter latency to enter the preference zone close to the larger shoal relative to the smaller shoal ($t_{83} = 3.961$, $p < 0.001$). Differences in performance cannot be attributed to different levels of locomotor activity, since no significant differences were exhibited in swimming activity among fish exposed to the different contras ($F_{6,77} = 1.611$, $p = 0.156$).

When comparing the results of Experiment 2 (contrasts in small number range) and Experiment 3 (contrasts in large number range), a significant difference was found in the magnitude of the preference for the larger shoal. Fish in Experiment 3 showed a significantly higher preference for the larger shoal than fish in Experiment 2 ($F_{1,154} = 4.916$, $p = 0.028$). A significant difference was also found when we pooled groups exposed to contrasts equaling or exceeding a ratio of 2:1 in Experiment 2 (four groups) with those exposed to the same ratios in Experiment 3 (four groups). In Experiment 3, fish exposed to shoals with ratios $\geq$2:1, spent significantly more time close to the larger shoals than did fish in Experiment 2 ($F_{1,94} = 4.601$, $p = 0.035$). However, no significant difference existed in the locomotor activity of fish in Experiment 2 and Experiment 3 ($F_{1,154} = 0.298$, $p = 0.586$). Furthermore, a significantly shorter latency to approach the preference zone close to the larger stimulus shoals was shown by fish of Experiment 3 relative to those of Experiment 2 ($F_{1,154} = 10.531$, $p = 0.001$).

Discussion

In this study, angelfish were required to remember previously seen shoals differing in the number of shoal members, a quantity discrimination task. The retention interval during which the experimental fish could not observe the contrasted shoals was doubled compared to the longest interval imposed before (Gómez-Laplaza and Gerlai 2016a, b), i.e., it was increased from 15 to 30 s. While this increase may not seem substantial, it led to an interesting dissociation between how angelfish discriminated shoals differing in number within the small number range and within the large number range.

We found that with a retention interval of 30 s, angelfish failed to discriminate in the comparisons involving shoals whose numerical size was in the small number range (maximum 4), but not when the two contrasted shoals had at least 4 members each and the ratio of these shoals was at least 2:1. The failure to distinguish shoals of different numerical size in the small number range contrasts with results previously obtained with angelfish (Gómez-Laplaza and Gerlai 2011b, 2015). Notably, in these latter studies, either no memory demand was placed on performance (Gómez-Laplaza and Gerlai 2011b) or the retention interval was not longer than 2 s (Gómez-Laplaza and Gerlai 2015). Importantly, imposition of the 30-s retention interval did not alter the performance of angelfish when the experimental subject was exposed to contrasts in the large (at least 4 items) number range. That is, irrespective of the length of retention interval (from 0 to 30 s), angelfish were able to discriminate the larger shoals in the large number range as long as the ratio of the contrasted shoals was at least 2:1. This is notable for two reasons. First, it shows that angelfish can reliably distinguish large quantities of

items (shoal members) under different conditions. Second, and most importantly, it also implies that the mechanisms underlying quantity estimation in the small versus the large number ranges may be distinct. Whether this distinctiveness concerns attentional, stimulus processing, cognitive or memory-related mechanisms is not known at this point.

In the past, some studies showed distinct abilities in comparing items in the small versus large number ranges in a variety of vertebrate species (see Feigenson et al. 2004; Uller 2008) including fish (Agrillo et al. 2008, 2012) and also angelfish (Gómez-Laplaza and Gerlai 2011b). The argument made in these studies has been that two distinct stimulus processing/cognitive mechanisms may exist: the object file system (OFS) for small numbers and the analogue magnitude system (AMS) for large number. OFS is associated with being able to follow individual items and is sensitive to absolute differences between the contrasted sets (but only up to and including 3 or, in some species, 4 items). AMS is employed for distinguishing large quantities (at least 4 items) frequently on the basis of non-numerical features that correlate with number, and performance using this system is affected by the ratio, and not the absolute numerical difference, between the contrasted quantities (see Feigenson et al. 2004). Nevertheless, other studies have presented results that could be explained by the use of a single system, the AMS, and argued against the existence of two distinct systems (e.g., Cantlon and Brannon 2006). Findings of our current study now go against this latter argument, as they suggest the existence of two separate discrimination systems, one that is sensitive to the longer (30-s-long) retention interval (the OFS) and another that is not (AMS).

Although not frequently tested, memory use in discrimination between sets differing in number of items has been reported in some animal species. For example, Beran and Beran (2004) reported that chimpanzees were successful in discriminating the larger set of bananas sequentially presented in two opaque containers over a 20-min presentation period. Since chimpanzees never saw more than one banana at a time, and they were never able to see the complete sets, results indicated long-term memory for quantity discrimination. The results obtained by Beran and Beran (2004) with chimpanzees suggested, in contrast to ours, similar performance in the small and large number range. Food-storing birds have also been found to possess remarkable numerical competence and memory for locations where more food items were hidden. A memory demand of up to 60 s was imposed in studies with North Island robins (*Petroica longipes*) which successfully retrieved the location of larger food quantities after this retention interval, even when food items were hidden from view in 2–4 different sites (Armstrong et al. 2012). Also, New Zealand robins (*Petroica australis*) were successful in

the large number range, choosing the larger quantity of food items sequentially presented and concealed from view (Hunt et al. 2008). Thus, the ability to discriminate between quantities even after a period of time of not seeing the actual items may be an adaptive response to ecological challenges faced by food-storing or scatter-hoarding birds. Nevertheless, different species facing idiosyncratic ecological challenges may not have evolved the same memory capabilities for quantity and/or spatial information. We have not tested retention intervals longer than 30 s in angelfish; therefore, we do not yet know the upper retention interval limit in this species. Similarly, we do not know whether memory performance is dependent upon behavioral context. For example, since angelfish have numerous predators in the wild (Praetorius 1932), it is likely that joining the larger shoal is adaptive, and thus, the ability to discriminate shoals based upon quantity or number has evolved. Furthermore, it is also plausible that only shoals in the large number range may provide appropriate protection against predators, and thus, an angelfish temporarily separated from such shoals will need to remember where the better (larger) shoal may be found. On the contrary, it may not be as important which shoal has more members when the number of members in the shoal is in the small number range. Thus, the importance of making the correct choice may be reduced and angelfish may not need a precise memory of shoals when these are small and differ only in a few members (e.g., Landeau and Terborgh 1986). We must note that lack of preference exhibited in particular contrasts does not necessarily mean inability to distinguish these contrasts. For example, we found angelfish not to show a significant preference for the larger of the two shoals in the 4 versus 1 contrast. It is possible that more sensitive (e.g., multiple-trial-bases training) tests would have found the apparent preference for the 4-member shoal significant. We also note that the 4 versus 1 contrast may be a special condition. It has resulted in conflicting findings in studies conducted with diverse animal species. Feigenson et al. (2002a) found human infants not to be able to discriminate 4 versus 1 items, and Hauser et al. (2000) found a similar result with rhesus monkeys. On the other hand, Cordes and Brannon (2009a) found the opposite, as in their study, human infants were able to discriminate the contrast 4 versus 1, and Cantlon and Brannon (2007) showed the same with rhesus monkeys. Unlike in our current study, successful discrimination of the 4 versus 1 contrast has also been found in different fish species (e.g., Stancher et al. 2013), including angelfish (Gómez-Laplaza and Gerlai 2011b). One possible explanation for these conflicting results may lie in the fact that the number 4 is at the boundary between the analogue magnitude and object file mechanisms. Thus, depending on specific experimental conditions (and perhaps species), it may fall on one or the

other side of the boundary. These are speculative arguments whose validity will have to be ascertained by examining predation risk experimentally.

Different performance for small and large numbers has been previously reported in a study with adult guppies (Agrillo et al. 2014). In that study, however, after a training period, guppies were tested with moving and static items and were able to discriminate moving items only in the small number range, whereas they were unsuccessful when tested with large numbers despite ratios being identical. On the contrary, in the current study a failure in the discrimination was obtained when small numbers were presented, whereas angelfish were successful with large numbers. Different procedures (training, i.e., multiple exposures to the test condition versus spontaneous discrimination, i.e., a single exposure to the test), type of stimuli (geometric figures vs. living conspecifics), fish species and other methodological details may account for the different results. Nevertheless, importantly, both the results of the Agrillo et al. (2014) study and those of our current study imply the existence of the two separate systems (OFS and AMS) underlying discrimination for small and large numbers.

We note, however, a complexity in our current results. The performance of angelfish exposed to the large number range contrasts did not strictly follow Weber's law. The preference index, i.e., the magnitude of preference for the numerically larger shoal, was not proportional to the ratio between the number of stimulus fish in contrasted shoals. For example, while the preference index was significantly above chance among fish of groups exposed to contrasts 12 versus 4, 10 versus 4, 10 versus 5, the performance in these groups was statistically indistinguishable, and not even a hint of correlation between the size of the performance index and the contrasted shoal number ratios was apparent (see Fig. 3). This lack of correlation in the large number range is in contradiction with our findings in previous studies in which we tested performance of angelfish under similar conditions with similar procedures and with a much shorter memory demand (2 s) (Gómez-Laplaza and Gerlai 2016a). Therefore, we speculate that the short-term memory encoded by angelfish includes information on where the shoals are and which shoal contains larger number of fish, but not necessarily on the actual relative difference between the contrasted shoals. That is, as long as the ratio is at least 2:1, angelfish will remember and respond to the numerically larger shoal similarly.

Last, we consider a potential confounding variable. During the tests, we allowed the experimental fish to view a single stimulus fish on each side. This method was previously employed to "entice" the test subjects to approach and stay in proximity of the stimulus zone. The argument was that because both of the contrasted sides had a single

stimulus fish, the setup was symmetrical, and the only source of potential side bias for the experimental fish should have been their memory of the previously viewed numerically different stimulus shoals. Nevertheless, one may argue that the single stimulus fish that remained visible during test may have behaved differently depending on whether they were on the side of the larger versus the smaller shoal. Although we cannot completely exclude this possibility, we argue that this explanation is unlikely for three reasons. First, the small space in which the single stimulus fish was confined did not allow this fish to exhibit a varied behavioral repertoire. Second, the stimulus fish were randomly assigned, and thus, individual differences among them could not have introduced a tendency in our data. Third, there is no known behavioral response of these stimulus fish that has been shown to be dependent upon how many other stimulus fish were in the other sealed part of the compartment during the stimulus fish exposure period.

Although our results demonstrated that angelfish can remember where the larger versus the smaller shoal was located in their environment, at least in the larger number range, what features of the different shoals the experimental subjects learned and remembered are not yet known. Furthermore, we note that our results do not distinguish numerical estimation from quantity discrimination. Non-numerical, continuous variables that covary with shoal size, such as swimming activity, shoal density, inter-fish distance and cumulative surface area, have all been shown to influence the discrimination of quantities in angelfish, suggesting that the discrimination of numerically distinct shoals may be dependent on quantitatively varying aspects of these shoals (Gómez-Laplaza and Gerlai 2012, 2013a, b). In other species too, non-numerical cues have been reported to influence quantity discrimination (Agrillo et al. 2010; Cordes and Brannon 2009b; Feigenson et al. 2002b; Frommen et al. 2009). Therefore, the memory for the location of larger and smaller shoals, demonstrated in our current study, does not prove, although still could be the result of, mental representation of numerical attributes of the shoals. Recently, Gebuis et al. (2016) have proposed that because numerical and non-numerical features of the stimuli are inextricably linked in most contexts and because of the difficulties of extracting numerosity independently of non-numerical visual cues, a more comprehensive explanation, a sensory-integration system for multiple features or pieces of information (density, surface, diameter, etc.) may need to be assumed. Gebuis et al. (2016) argued that such a feature integration system may better account for the often conflicting results found in the literature. Furthermore, the manner in which specific features that covary with item number influence quantity discrimination may be highly context dependent, and how

these features may be used in combination may be best described using a differential weighing system. That is, each feature may have a weight and depending on the size of this weight may play a greater or smaller role in quantity discrimination performance under certain behavioral contexts or in response to specific experimental procedures.

In summary, our results demonstrate that angelfish can learn and remember the location of larger versus smaller shoals in their environment. This memory was successfully acquired by angelfish for shoal sizes in the larger number range, i.e., for shoals that had 4 or more individual members and also differed by twofold in terms of the number of fish in them. A similar memory for numerically smaller shoals could not be found in the current study. These findings, together with prior results, lend support for the existence of two distinct quantity discrimination systems: the object file system for small number of items and the analogue magnitude system for large number of items. Although we do not know what features of the shoals angelfish actually learned and remembered, and we also do not know why Weber's law did not strictly apply for the memory-dependent discrimination of angelfish in the large number range, these results open exciting new avenues of research into what this simple teleost, the angelfish, learns about numerically distinct quantities and how it remembers the learned information.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval The experiments described here comply with the current law of the country (Spain) in which they were performed, and were approved by the Committee on the Ethics of Animal Experiments of the University of Oviedo (permit number: 13-INV-2010).

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